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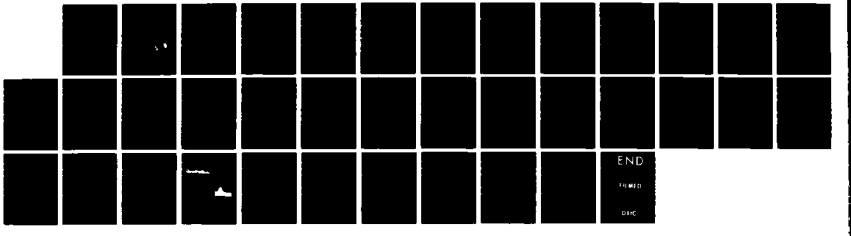

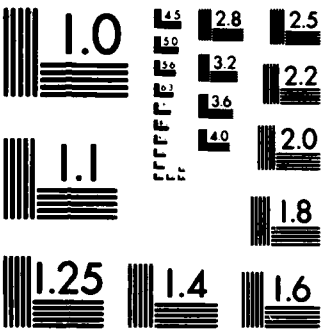

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strengthen or weaken the synaptic connectivities. The functional dependence of these mechanisms on the postsynaptic activity is shown to determine whether the neuron acts as an S-cell or a G-cell. A circuit is proposed for a module that consists of a G-cell and several S-cells sharing a common set of inputs. By inhibiting the G-cells, the S-cell acts as a contrast-enhancing element, increasing their specificities for individual patterns in the stimulus set. The output from the module is a recorded representation of the environment with respect to its general and distinctive features.

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A Model for Generalization and Specification by Single Neurons *

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Abstract. A rule for environmentally dependent modification of the neuronal state is examined. Under the rule, the neuron selects a trigger feature that matches either a particular pattern in the stimulus set, or the most common pattern component, depending on a certain parameter. Thus a neuron may evolve to respond to its stimulus environment in one of two capacities, namely *specification* or *generalization*. Neurons of the former variety are labelled "S-cells"; and those of the latter, "G-cells". In the model, synaptic modification is modulated by two postsynaptic mechanisms, which act antagonistically to strengthen or weaken the synaptic connectivities. The functional dependence of these mechanisms on the postsynaptic activity is shown to determine whether the neuron acts as an S-cell or a G-cell. A circuit is proposed for a module that consists of a G-cell and several S-cells sharing a common set of inputs. By inhibiting the G-cells, the S-cell acts as a contrast-enhancing element, increasing their specificities for individual patterns in the stimulus set. The output from the module is a recoded representation of the environment with respect to its general and distinctive features.

1. Introduction

1.1. Trigger features

Barlow (1972) expresses the importance of single neuron response characteristics as perceptual substrates. He stresses the role of a sensory neuron's "trigger features" which, according to that paper's third proposition,[1] "are matched to redundant patterns of stimulation by experience as well as by developmental processes." The present paper is concerned with the following question: To *which* of the redundant patterns in a neuron's stimulus environment is its trigger feature(s) matched, and *how* (in a mathematical sense) can this match evolve with experience?

Several theories describe the evolution of neuronal trigger features (e.g. von der Malsburg, 1973 ; Perez et al., 1975 ; Grossberg, 1976 ; Amari and Takeuchi, 1978). In the present paper, a scheme for neuronal plasticity is put forward in which neurons dynamically adapt to their individual stimulus environments such that some tune to particular patterns (specification) while others tune to the most prevalent pattern *component* (generalization). The model extends the theory of Bienenstock et al. (1982) for development of orientation selectivity in visual cortex to yield either maximization or minimization of selectivity, depending on the relation between two antagonistic mechanisms that postsynaptically modulate synaptic plasticity. If the functions are of the same form, this relation can be expressed in terms of a (fixed) neuronal parameter. By developing response characteristics to have low selectivity, the neuron generalizes by matching its trigger feature to the component most common among the stimuli in its environment, that *component* being a redundant pattern of stimulation as in Barlow's third dogma. On the other hand, by pursuing a highly specific response function, the trigger feature evolves to match a particular pattern, while ignoring a maximally broad range of the remainder of the stimulus set. Thus some neurons pursue common features and some pursue distinctive features in the environment.

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[1] Barlow's paper consists of five speculative propositions (dogmas) which he supports with persuasive arguments and substantial experimental data.

1.2. Physiological evidence

The development of highly selective neurons in mammalian visual cortex (particularly in cats and monkeys) has been extensively studied under variously restrictive rearing conditions and has been shown to depend critically on the visual environment (for a comprehensive review of the literature, see Movshon and Van Sluyters, 1981). The stimulus parameters over which selectivity has been shown to develop have generally been orientation and spatial frequency. However Gross et al. (1972) found neurons in the pre-striate cortex of macaque monkeys tuned to features of higher specificity such as hands and faces.

Cortical neurons exhibiting low or zero selectivity in the orientation domain have also been observed. These are particularly common in layer 4 of monkey striate cortex (Hubel and Wiesel, 1977). If such neurons are present in the cat, they are certainly less common. Kelly and van Essen (1974) report symmetric receptive fields in some units but classify them as geniculate afferents. Palmer and Davis (1981), on the other hand, give evidence that nonselective cortical neurons exist in cat visual cortex, but are rare.[2]

2. The model

This section includes the formal description of the model and some analysis of its structure. No argument is presented in this paper to motivate the mathematics. Interested readers should consult Cooper et al (1979) and Bienenstock et al (1982). Vector quantities appear in bold type and are specified by superscripts. Components of vectors are not in boldface and are identified by subscripts. Let $d_i(t)$ label the i-th stimulus component, a measure of the activity of the i-th afferent at time t. Corresponding to each component is a synapse of strength $m_i(t)$. There are N components to both **d** and **m**, hence they are both vectors in N-space, or *synapse space*. A stimulus *environment* refers to a probability density for **d** in N-space.

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[2] In this study of single neuron response properties in cortex, 13 units from a total of 257 were found not to be orientation-selective. On the basis of their response properties, 9 were thought to be geniculocortical (LGN Y-cell) afferents. Palmer and Davis conclude that the remaining four are nonselective cortical neurons.

2.1. The transfer function

Let the net integrated depolarization $x(t)$ be the thresholded linear expression:

$$x(t) = \max\left(0\,,\ \sum_{i=1}^{N} m_i(t)d_i(t)\right) \tag{1}$$

The response frequency $c(x)$ of the neuron is thought to be increasing in x and linear in some region, but with nonlinearities for x low (the firing threshold) and x high (maximum firing rate). Since x rather than c is used in the learning rule, the precise form of $c(x)$ is not important. The input-output relation is determined by the synaptic weights m_i, hence the input activity levels d_i are termed *presynaptic* and the output activity x (or c) is termed *postsynaptic*.

A neuronal variable, $q(t)$, is involved in the synaptic plasticity rule and will be defined later. Together, the synapse vector $\mathbf{m}$ and the value $q(t)$ make up the *neuronal state* $(\mathbf{m},q)$, an (N+1)-dimensional quantity. For simplicity, the components m_i function as "ideal synapses" (Nass and Cooper, 1975) capable of changing sign. A treatment is given in the discussion (section 4.2.2) in which the signs of the synaptic weights does not change.

2.2. The modification rule

The rule for neuronal plasticity describes the changes in $\mathbf{m}$ and q as time derivatives:

$$\dot{m}_i(t) = \phi(x,q)d_i(t) \tag{2a}$$

$$\dot{q}(t) = \beta\phi(x,q)x(t) \quad ; \quad \beta>0 \tag{2b}$$

$$\textit{where} \quad \phi(x,q) = \sigma_2(x) - q\sigma_1(x) \tag{2c}$$

The postsynaptic[3] modulatory function $\phi(x,q)$ is given in terms of q and two continuous, monotone increasing functions of x: $\sigma_1(x)$, and $\sigma_2(x)$. To complete the rule, the following restrictions are imposed. The function ϕ is subject to the condition $\phi(0,q)=0$ for all $q>0$. Consequently, the two functions σ_1 and σ_2 must each vanish for $x=0$. Also, for any fixed value $q>0$, σ_1 and σ_2 are to be such that there exist at most one other value $x>0$ at which

[3]Rules for synaptic modification are often expressed as the product of a function of the presynaptic activity and a function of the postsynaptic activity. This approach dates back to Thorndike's (1913) "Law of Use" and Hebb's (1949) "Neurophysiological Postulate", but has not been experimentally verified until recently (Levy and Steward, 1979; Rauschecker and Singer, 1981; Singer, 1982; Singer and Rauschecker, 1982).

$\phi(x,q)=0$. The parameter β specifies a rate constant for $\dot{q}$ relative to $\dot{\mathbf{m}}$. In the simulations below, β has been set to unity.

2.2.1. Parallel modification

Consider the above equation (2a) for $\dot{\mathbf{m}}$ and note that it is linear in the stimulus $\mathbf{d}(t)$. The modification to $\mathbf{m}$ induced by a given stimulus is thus parallel or antiparallel to $\mathbf{d}$. Of all possible input stimuli of a given magnitude, the response to the one in the direction of that stimulus $\mathbf{d}$ is most greatly affected by the change in $\mathbf{m}$. Therefore parallel modification (linearity of $\dot{\mathbf{m}}$ in $\mathbf{d}$) has the following behavioral implication for a system: *learning induced by a particular stimulus more greatly influences future responses to that stimulus than to others of the same magnitude.*

The sign of the function ϕ determines whether the synapses get stronger or weaker -- i.e. whether $\dot{\mathbf{m}}$ is parallel or antiparallel to $\mathbf{d}$. For a given value of q, ϕ has at most two zeros in x, one of them being $x=0$. Thus the sign of ϕ can vary over x in four ways, depending on the value of q. Two of these are illustrated in Figure 1a in which for q sufficiently small or large and $x>0$, ϕ is respectively positive or negative definite. For intermediate values of q, ϕ is first positive and then negative (Figure 1b) or vice versa (Figure 1c). These last two situations can be labelled by the sign of the partial derivative ϕ_x at the point $x=\theta(q)>0$ where $\phi(\theta(q),q)=0$. That sign depends strictly on the forms of $\sigma_1(x)$ and $\sigma_2(x)$ and hence only one of these two cases is possible for a given neuron.

2.2.2. Restrictions on σ_1 and σ_2

As shown in Figure 1, cross sections of $\phi(x,q)$ at constant q can evolve in just two ways as q increases from 0. For q less than or equal to a certain value q_a, ϕ is always positive for $x>0$, and for $q \geq q_b$, ϕ is always negative. Thus a function $\theta(q)$ can be defined on the interval $q \in (q_a,q_b)$ such that $x=\theta(q)>0$ is the second zero of ϕ -- i.e. $\phi(\theta(q),q)=0$. The inverse function $q=\theta^{-1}(x)$ is given by:

$$\theta^{-1}(x) = \frac{\sigma_2(x)}{\sigma_1(x)} \tag{3}$$

The following theorem establishes a condition on σ_1 and σ_2 that allows $\phi(x,q)$ at most one zero on the domain $x>0$ for any fixed value of q.

Theorem. For any fixed positive value of q, the function $\phi(x,q)=\sigma_2(x)-q\sigma_1(x)$, where $\sigma_1(x)$ and $\sigma_2(x)$ are positive and differentiable on the domain $x>0$, has at most one zero for $x>0$ if the Wronskian $W(\sigma_1(x),\sigma_2(x))$ is either always positive or always negative for $x>0$.

Proof. For a fixed positive value of q, define a set of values x_i on the domain $x>0$ such that $\phi(x_i,q)=0$ for all i. If the sign of the partial derivative $\phi_x(x=x_i)$ is constant for all values of $x>0$, then there can only be one zero of ϕ in that domain. Note that $q=\sigma_2(x_i)/\sigma_1(x_i)$ for all i. $\phi_x(x=x_i)$ is shown to be equal to $\frac{W(x)}{\sigma_1(x)}$:

$$\begin{aligned}\phi_x(x=\theta(q)) &= \sigma_2' - \frac{\sigma_2}{\sigma_1}\sigma_1' \\ &= \frac{1}{\sigma_1}\begin{vmatrix}\sigma_1 & \sigma_2 \\ \sigma_1' & \sigma_2'\end{vmatrix} \\ &= W(\sigma_1,\sigma_2)/\sigma_1\end{aligned} \tag{4}$$

Hence the sign of $\phi_x(x=\theta(q))$ is the same as the sign of $W(x)$. This completes the proof.

The (constant) sign of $W(x)$ will be shown to determine the feature abstracting property of the neuron. If $W(x)$ is always positive, the neuron *generalizes* (a "G-cell") and if it is negative the neuron tunes to a *specific* stimulus (an "S-cell"). This is demonstrated in Section 3. The sign of $\theta'(q)$ is constant for all values of $q\in(q_a,q_b)$ and is also the same as those of $W(x)$ and $\phi_x(x=\theta(q))$. This is because the inverse function $\theta^{-1}(x)$ is also monotone increasing or decreasing:

$$\frac{d\theta^{-1}(x)}{dx} = \frac{\sigma_1\sigma_2'-\sigma_1'\sigma_2}{\sigma_1^2} = \frac{W}{\sigma_1^2} = \frac{\phi_x(\theta,q)}{\sigma_1} \tag{5}$$

In addition to the signs of ϕ_x, $W(x)$, and $\theta'(q)$, there is a fourth quantity providing an equivalent condition. Those three quantities are positive if and only if the logarithmic

derivative (LD) of $\sigma_1(x)$ is greater than the LD of $\sigma_2(x)$ for all $x>0$, and negative if and only if the reverse condition holds. Thus the LD of one function is required to be consistently higher than the other. The feature abstracting property of the neuron depends only on *which* LD is greater.

2.2.3. Some allowed functions

Now consider functions σ_1 and σ_2 that can be expressed as a common function, only with different scale parameters:

$$\sigma_i(x) = \mu_i \sigma(\frac{x}{\eta_i}) \tag{6}$$

The sign of the Wronskian is now related to a functional of $\sigma(x)$ by the following corollary. Note that the amplitude parameters μ_1 and μ_2 are not important here since neither the sign of the Wronskian nor the logarithmic derivatives depend on them.

Corollary. The function $\phi(x,q)=\sigma(x/\eta_2)-q\sigma(x/\eta_1)$ has at most one zero for $x>0$ if $L[\sigma(x)]>0$ for all $x>0$, where $L[\sigma(x)]=x(\sigma'(x))^2-x\sigma(x)\sigma''(x)-\sigma(x)\sigma'(x)$. If this condition holds, then the sign of the Wronskian $W(\sigma(x/\eta_1),\sigma(x/\eta_2))$ equals $\mathrm{sgn}(\eta_2-\eta_1)$.

Proof. If the LD of $\sigma(x/\eta)$ is monotone increasing in η, then the LD for the sigma function with a higher value of η will always be greater. Thus a derivative is taken with respect to η and the sign of the result is seen to be equal to the sign of $L[\sigma(x)]$:

$$\frac{d}{d\eta}\left[\frac{\sigma'(x/\eta)}{\eta\sigma(x/\eta)}\right] = \frac{-s\sigma(s)\sigma''(s)+s(\sigma'(s))^2-\sigma'(s)\sigma(s)}{(\eta\sigma(s))^2} \tag{7}$$

where $s=\frac{x}{\eta}$

The case for negative definite $L(x)$ (for which the signs are opposite) can be ruled out by considering the behavior of $\phi(x,q)$ for $q=\mu_2/\mu_1$ in the neighborhood of $x=0$. In this case, ϕ has the same sign as $\sigma(x/\eta_2)-\sigma(x/\eta_1)$. Hence, as x increases from zero, ϕ takes on the sign opposite to $\eta_2-\eta_1$. Note that for $0<x<\theta(q)$, the sign of ϕ must be opposite to that of the Wronskian. Therefore only the case in which the LD increases with η applies, so the condition $L(x)>0$ is sufficient and the signs of the Wronskian etc. are equal to $\mathrm{sgn}(\eta_2-\eta_1)$.

Certain functions used to approximate the relation between net somatic depolarization and neuronal firing rate (i.e. $c(x)$) satisfy this corollary. Among such functions are $\ln(1+x)$ (Agin, 1964) and sigmoidal functions of the form:

$$\sigma(x)=\frac{x^p}{x^p+1} \quad p \geq 1 \tag{8}$$

which approximate typical bounded threshold functions like that measured by Chapman (1966) in the crab and by Creutzfelt et al. (1970) in cat retinal ganglion cells. Hence either σ_1 or σ_2 might be related to the firing rate c.

For the case where σ_1 and σ_2 are of the same form $\sigma(x/\eta)$, the sign of the Wronskian is seen to depend on which function has the greater scale factor η for the argument. Thus $\mathrm{sgn}(W(x))=\mathrm{sgn}(\eta_2-\eta_1)$, and so for $\eta_2>\eta_1$ the neuron tunes to a particular stimulus in its stimulus environment, and for $\eta_2<\eta_1$ the neuron is driven towards generalization.

2.3. Stability

Trajectories are drawn in the $m-q$ plane for a one-synapse neuron receiving a constant stimulus $d_0=1$ (Figure 2). It can be seen that the neuron is always driven to a finite final state. Note that if the initial value of q is too large the final value of m will be zero (the neuron loses all responsivity).[4] The final states of the system are not perturbed by small amounts of signal noise on the average. This is because the expected value of $(\dot{m},\dot{q})$ is along a trajectory. Consider noise uniform on the interval $[-a,a]$:

$$\mathrm{E}\left[\begin{pmatrix}\dot{m}\\ \dot{q}\end{pmatrix}\right] \approx \frac{1}{2a}\int_{-a}^{a}\phi_x(m_0d_0,q_0)m_0\epsilon\begin{pmatrix}(d_0+\epsilon)\\ \beta m_0(d_0+\epsilon)\end{pmatrix}d\epsilon \tag{9}$$

$$= \frac{a^2}{3}\phi_x(m_0d_0,q_0)m_0\begin{pmatrix}1\\ \beta m_0\end{pmatrix}$$

Hence perturbations from equilibrium states are, on the average, driven back to the same equilibrium point in the m-q plane.

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[4] Hence it may be advantageous to assume that $q(t=0)=0$. It should be noted however that this condition is not sufficient for multi-pattern environments. Simulations indicate that the initial values of the synaptic weights must be large in order to guarantee a nontrivial final state.

3. Feature abstraction

The dependence of a neuron's feature abstraction properties (specification or generalization) on the sign of the Wronskian has already been mentioned. The degree of selectivity and the quality of feature abstraction depend critically upon the structure of the stimulus environment in N-space. Therefore selectivity is precisely (albeit somewhat arbitrarily) defined and discussed in this section for a variety of pattern sets and the feature abstraction properties of the model are analyzed.

3.1. Stimulus environments and selectivity

It is important to emphasize the role of the neuron's stimulus environment as a context for both the development and testing of neuronal response characteristics. Since each stimulus can be represented in the same N-dimensional space as the synaptic state $\mathbf{m}$, a stimulus environment can be thought of as a probability density function on that space. Under a given learning rule, the locus of stable (final) states $\mathbf{m}(t \to \infty)$ is determined by the stimulus environment.

Neuronal selectivity is measured with respect to a *test environment*, a set of stimuli which one must be careful to distinguish from the *learning environment*. While the neuronal state may undergo a measurable (adaptive) change under the influence of the learning environment (indeed this is often the whole point), the test environment is used to perform a *measure* on the state. Even so, in the analysis of this model the learning environment is virtually identical (except for the addition of a random noise term) to the test environment. Also, the inevitable influence of the measurement on the state itself is idealized to be nil.

A neuronal response function $c(\mathbf{m},E)$ can be calculated over any pattern set E for a given synaptic state $\mathbf{m}$. A precise definition of selectivity for a general stimulus density function $P(dE)$ was given by Bienenstock (1980). This can be paraphrased:

$$S(\mathbf{m},E) = 1 - \frac{\int_E c(\mathbf{m},E)P(dE)}{c_{max}} = 1 - \frac{c_{avg}}{c_{max}} \qquad (10)$$

where $c_{max} = \max_E(c(\mathbf{m},E))$

Note that $S(\mathbf{m},E) \in [0,1)$ with zero indicating a uniform response across E and unity being an idealized (zero-width) response peak. The function is illustrated (Figure 3) for a stimulus environment that is characterized in terms of a single parameter.

For a given environment E, the selectivity $S(\mathbf{m},E)$ is a scalar function of the state $\mathbf{m}$. In Figure 4, lines of constant selectivity are plotted for an environment consisting of two discrete patterns $\mathbf{d}^1$ and $\mathbf{d}^2$. Restrictions on the synapses, such as the sign of m_i, may prevent a cell from realizing its optimal state. In such cases, simulations have indicated that the neuronal state is driven to the limiting boundary.

3.2. Discrete pattern sets

3.2.1. Two patterns in two dimensions

This is the simplest case in which the feature abstraction properties of the model can be analyzed. The neuronal state space is illustrated in Figures 5a and 5b. For each pattern there exist two surfaces at which $\phi=0$. One surface is the plane $\mathbf{m}\cdot\mathbf{d}=0$ and the other surface represents the relation $\mathbf{m}\cdot\mathbf{d}=0(q)$. At the intersections of the $\phi(\mathbf{m}\cdot\mathbf{d}^1,q)=0$ surfaces and the $\phi(\mathbf{m}\cdot\mathbf{d}^2,q)=0$ surfaces are equilibrium states where $\phi=0$ for both patterns.

There are four distinct loci of equilibrium states. One consists of the q-axis ($m=0$), two represent maximally selective states (one for each pattern), and one is made up of states having minimum (zero) selectivity. In the case where the Wronskian is positive, only points belonging to the maximally selective equilibrium locus are stable and if the Wronskian is negative only the minimally selective (nontrivial) equilibrium points is stable.

For a given synaptic vector $\mathbf{m}$, ϕ is positive for $q<\theta^{-1}(\mathbf{m}\cdot\mathbf{d}^1)$ and $q<\theta^{-1}(\mathbf{m}\cdot\mathbf{d}^2)$ – i.e. below both surfaces $\mathbf{m}\cdot\mathbf{d}^i=0(q)$ (cf Figure 2). Above the two surfaces, ϕ is negative. Hence in such cases the neuronal state is driven toward those surfaces and eventually ends up between them, at their intersection (zero selectivity), or on the q-axis ($\mathbf{m}=0$). These cases are considered below.

Case 1: $\theta^{-1}(\mathbf{m}\cdot\mathbf{d}^1) > q > \theta^{-1}(\mathbf{m}\cdot\mathbf{d}^2)$. The argument for this case can also be applied to the case where $\mathbf{d}^1$ and $\mathbf{d}^2$ are reversed. Here $\phi(\mathbf{m}\cdot\mathbf{d}^1) > 0$ and $\phi(\mathbf{m}\cdot\mathbf{d}^2) < 0$, so the response $\mathbf{m}\cdot\mathbf{d}^1$ tends to increase and the response $\mathbf{m}\cdot\mathbf{d}^2$ tends to decrease. This drives the state toward minimum selectivity (i.e. toward $\mathbf{m}\cdot\mathbf{d}^1 = \mathbf{m}\cdot\mathbf{d}^2$) if $\mathbf{m}\cdot\mathbf{d}^1 < \mathbf{m}\cdot\mathbf{d}^2$, and toward maximum selectivity (in this case toward $\mathbf{m}\cdot\mathbf{d}^2 = 0$) if $\mathbf{m}\cdot\mathbf{d}^1 > \mathbf{m}\cdot\mathbf{d}^2$. Therefore the feature abstraction property of the neuron depends on the sign of $\theta'(q)$ (and hence on the signs of $W(x)$ and $\phi_x(x = \theta(q))$ as shown earlier in (5)).

Case 2: $\mathbf{m}\cdot\mathbf{d}^1 = \mathbf{m}\cdot\mathbf{d}^2 = \theta(q)$. In this case the neuron is in a minimum selectivity equilibrium state and so the stability of the state must be considered. Any noise in the stimulus, response, or plasticity function will perturb the state from equilibrium. By the above arguments it is seen that an S-cell will be driven away from this locus and a G-cell back toward it.

Case 3: $\mathbf{m}\cdot\mathbf{d}^1 = \mathbf{m}\cdot\mathbf{d}^2 = 0$ (the q-axis). The q-axis is a locus of trivial (zero response to all stimuli) states which is stable for $q \geq \theta^{-1}(x = 0)$. However it is never reached (again see Figure 2) if the initial value of q is small ($q(t = 0) << \theta^{-1}(x = 0)$).

m-plane projections of numerically evaluated trajectories are shown in Figure 6 for 2-pattern environments.

3.2.2. Linear Independence

A linearly independent set of K stimulus patterns presented to a neuron stochastically is treated as an ideal case, since the model can function perfectly in this situation. If each pattern is presented with non-zero probability, then neurons of both types will asymptotically approach their optimal selectivities: zero for G-cells and $1-1/K$ (the maximum) for S-cells. While this statement has not been proven, it is strongly supported by computer simulation. These ideal final states are possible for a linearly independent stimulus environment and *only for* such an environment. This can be seen by considering the synapse space. The conditions $\mathbf{m}\cdot\mathbf{d} = 0$ for $K-1$ patterns and $\mathbf{m}\cdot\mathbf{d} > 0$ for the last one (maximum selectivity) can only be simultaneously satisfied only if all K patterns are independent. Similarly, linear independence is required to reach zero selectivity nontrivially – i.e. to satisfy the condition that $\mathbf{m}\cdot\mathbf{d}$ be

constant for all environmental stimuli **d**.

An important feature of the model can be seen in such an environment (and proven for 2 patterns), namely that the neurons (asymptotically) acheive optimal selectivity *even if the patterns are not presented with uniform probability*. This is perhaps more impressive with respect to the generalizing neurons. A scheme whereby the synapses simply average the stimuli over time will extract the most common feature components *according to the probability distribution*. However, in this model the most common feature component *among the individual stimuli* is extracted.

3.2.3. Linear dependence

In general, the above "ideal" final states cannot be do not exist for an environment in which the stimuli are not independent. Nevertheless, both cell types are driven toward optimal states under this condition. For S-cells, a high selectivity is attained except under overwhelming circumstances, such as the situation in which all stimulus patterns differ only in their magnitude.[5] If all stimulus components are assumed to be positive, it is even difficult to design an environment under which the G-cell cannot reach a low-selectivity state. This is because for patterns having little in common (and therefore not very "generalizable"), all the synapses can simply grow very large so that just about any stimulus evokes a high response. The principal danger in this situation is *overgeneralization*: ideally, a G-cell will only respond with low selectivity as measured across its stimulus environment.

3.3. Continuous pattern sets

Certainly not all stimulus sets are discrete. For example, physical stimulus feature dimensions are almost all continuous since they are intensity measures. In this section continuous stimulus environments that have a periodic dependence on one or two parameters are dis-

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[5] Such pattern sets can be thought of as a single pattern, in that the informational content of a stimulus is contained in the *relative values* of the components. Thus the direction of a vector (stimulus or synaptic) is associated with information and the magnitude with intensity. Gati and Tversky (1982) relate these to the "qualitative" and "quantitative" aspects of a stimulus. Note that to incorporate this notion into the present model would require that the operant definition of selectivity be modified.

cussed. This is done as an approximation to a visual environment consisting of oriented contrast edges where *stimulus orientation* is the varying parameter. Because they have been widely used to measure the selectivity properties of neurons in striate cortex, such environments are useful for comparison of the model with experiment.

3.3.1. Periodicity in one parameter

The behavior of the model in an environment varying periodically in a single parameter provides a good illustration of how the model functions. Such environments map onto closed loops in N-space. Here these are assumed to be "reasonably" convex so that if two patterns are close in the stimulus space, then they are also close in terms of the environmental parameter (the converse holds for a continuous environment by definition). The principle of parallel modification operates in such an environment such that as the various patterns stimulate the cell they have the following cumulative effect. The selectivity-maximization property of the S-cell functions by "encouraging" patterns that evoke responses greater than $\theta(q)$ and "discouraging" patterns that evoke smaller responses (upper part of Figure 7). As q varies according to (2), the threshold and the response converge such that some responses lie above the threshold and others below. The neuronal response curve then becomes "separated" (i.e. the difference between the minimum and maximum response increases) about the threshold $\theta(q)$. In the lower part of Figure 7, the reverse process is seen to drive the response curve toward low selectivity.

3.3.2. Periodicity in two parameters

A pattern set periodic in two independent parameters has a more complex structure. The environmental topology progresses from a closed loop to a torus with the dependence on an additional parameter. The behavior of the model has not been treated analytically, but nonrigorous results have been obtained by numerical methods (Figure 8). These simulations indicate that the response surface of a G-cell becomes flat and that of an S-cell becomes peaked -- i.e. the cell types respectively seek minimum and maximum selectivity over *both* parameters.

4. Discussion

4.1. q as a time average over $x(t)$

This model is an extension of the Bienenstock et al. (1982) theory for selectivity maximization. In that theory the function ϕ is postulated to be a function of the instantaneous response c and the mean response $\bar{c}$. For a given value of $\bar{c}$, ϕ is negative for c below a certain threshold value θ and positive for $c>0$, where θ depends on $\bar{c}$. The system is stable for functions $\theta(\bar{c})$ that increase in a "faster-than-linear" fashion with $\bar{c}$ (e.g. $\theta(\bar{c})=\bar{c}^p$; $p>1$).

A more direct extension of that theory to selectivity minimization is possible (Munro, 1983), by inverting the requirements on the sign of ϕ and on the form of θ so that it is "slower-than-linear" in $\bar{c}$ (ie. $p<1$). Hence the important mathematical conditions on the model appear to be that ϕ change sign *once* as a function of the response and that the value θ vary temporally with the response according to a function which must satisfy certain conditions. The feature abstracting property of a given neuron then relies on the signs of two parameters, namely $\phi_c(c=\theta(\bar{c}))$ and $p-1$. Of the four possible combinations, one gives specification, one gives generalization, and the others do not converge to stable final states. Hence the following condition is imperative: $\mathrm{sgn}(\phi_c(c=\theta(\bar{c})) = \mathrm{sgn}(p-1)$. The interdependence of these two parameters is not so artificial in the approach taken by the present paper.

It has been shown that $\phi_x(x=\theta(q))$ and $\theta'(q)$ are related (5). The success of the model and its similarity to the theory of Bienenstock et al. depend on $q(t)$ playing the role of $\bar{c}$. By integrating (2b), one can see that q, like $\bar{c}$, is a time average of a measure of the postsynaptic activity:

$$q(t) = q_0 e^{-\beta\int_0^t x(t'')\sigma_1(x(t''))dt''} + \beta\int_0^t e^{-\beta\int_{t'}^t x(t'')\sigma_1(x(t''))dt''}\sigma_2(x(t'))x(t')dt' \qquad (11)$$

Note that the first term decays with time.

4.2. Visual cortex

4.2.1. Simulation of experiments

Since this model is a direct descendant of the theory of Bienenstock et al. (1982) for selectivity maximization in visual cortex (see Section 4.1), it comes as no surprise that the scheme for the S-cell explains the same body of physiological data. Computer simulation indicates that the two theories behave nearly identically, from a qualitative standpoint, in several variously manipulated visual environments (e.g. normal rearing, monocular and binocular deprivation, and reverse suture). However results differ for simulation of the artificial strabismus paradigm. A toroidal environment (section 3.3.2) is used to describe strabismic input. Recall that the S-cell tunes independently with respect to both parameters – i.e. it develops high specificity in both eyes, but not necessarily to a common pattern. In the Bienenstock et al. formulation, such an environment drives a neuron to a monocular state (Munro, 1983). That is, tuning is accomplished with respect to one of the two parameters. These results are purely empirical and have not been derived, so it is conceivable that the behavior of either or both models in a noncorrelated binocular pattern space depends on some parameter(s). Data from Hubel and Wiesel (1965) suggest that strabismic rearing results in fewer binocular cells, and thus supports the scheme of Bienenstock et al. as a model for visual cortex neurons. On the other hand, Blakemore and Van Sluyters (1974) report the existence of binocular neurons with a high orientation disparity between the two eyes.

4.2.2. Contrast enhancement

It is generally accepted that the projection from the principal visual input (the lateral geniculate nucleus of the thalamus) to striate cortex is overwhelmingly, and perhaps exclusively, excitatory. Inhibitory influence is therefore thought to be mediated by cortical interneurons. Figure 9 presents a scheme which is in accordance with these observations. A set of neighboring neurons is shown that share a common set of excitatory afferent fibers. A variety of S-cells serve to tune to a corresponding selection of environmental stimuli, whereas fewer G-cells are

required (perhaps only one).

By inhibiting all the S-cells in this "cluster", the G-cell can increase their selectivities. Inhibition by a G-cell raises the excitation threshold of an S-cell uniformly in as much as the response of the G-cell is uniform across the environment. A similar circuit has been proposed by Grossberg (1976). He proposes a scheme in which the inhibitory interneuron receives inputs from the surrounding feature detectors. The resulting response is of minimal selectivity to the extent that the input weights are equal.

Secondary evidence for such a circuit is found in the visual cortex of macaque. Hubel and Livingstone (1982) and Tootell et al. (1982) have found periodic clusters of non-selective cells centered in ocular dominance columns. Also, Hendrickson et al. (1981) report a similar distribution for the enzyme glutamic acid decarboxylase (GAD) which synthesizes the inhibitory neurotransmitter GABA. They have found localized GAD-rich areas that run parallel to ocular dominance columns. An examination of the fine structure of the axon terminals of low-selectivity neurons would directly test the hypothesis that they are inhibitory.

4.3. System organization

A conjecture can now be made explicit in terms of four neuronal types, defined according to their optimal selectivities (minimum or maximum) and their influence on other neurons (excitatory or inhibitory), namely that a circuit can be constructed from these four neuronal types (S^+,S^-,G^+,G^-) that will evolve to classify any stimulus set in terms of similarities and differences. That is, such a neural network might self-organize such that a taxonomic representation of the environment is constructed. This hypothetical network is not easily realized. The problem is to discover an architecture that provides an appropriate context for each neuron. Since this problem has not been solved, let us consider how it might be approached.

An initial step is to investigate the properties of small local neuron circuits or modules as discussed by several authors including Mountcastle (1978) and Szentagothai (1975). The contrast enhancement scheme in Figure 9 is a candidate for such a functional unit. The problem of how these modules might be arranged to form larger components must also be eventually

addressed. At each level the circuits are presumably genetically coded structures, within which individual neurons adapt to informational aspects of their respective stimulus environments.

Consider a system organized in a hierarchical fashion, reflecting progressively complex perceptual stages (e.g. sensation - recognition - association - cognition ...). It would be a mistake to assume that these stages lie in a strictly serial path since system processing is certainly parallel to a certain degree. The combined hierarchical/parallel flow of information in the visual system has been recently examined by Van Essen and Maunsell (1983) in terms of so-called "functional streams".

The nature of the stimulus environments at successive stages of neural processing probably becomes increasingly discrete. Shepard and Podgorny (1975) point out that symbolic stimuli are discretely coded while physical (nonsymbolic) stimuli vary continously along one or several dimensions: "For, whereas we can continuously shift a color (for example, blue) in brightness, hue, and saturation until it becomes as similar as we wish to any other color (for example, green), we cannot continuously deform a word 'blue' to another word 'green' without passing through intermediate configurations that are not words at all." Thus it is expected that inputs to the higher (more "gnostic") stages are more distinctly separated than early (sensory) input patterns. Inhibition is a powerful tool for separating patterns (see section 4.2.2) and as such may play an important role in the formation of discrete (symbolic) representations.

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Figure Captions

Figure 1. Functions $q\sigma_1(x)$, $\sigma_2(x)$, and $\phi(x,q)$ are plotted against x for two values of q ($q_1 < q_2$) in three situations. $q\sigma_1$ and σ_2 are shown above and ϕ is shown below. **a** $q_1 < q_a$; $q_2 > q_b$. **b** Both values of q in the interval $q \in (q_a, q_b)$ for a case where the Wronskian $W(\sigma_1,\sigma_2) < 0$. **c** The same for $W(\sigma_1,\sigma_2) > 0$. (See theorem in text). Note that the sequence of zero crossings for $\phi(x,q_1)$ and $\phi(x,q_2)$ in **c** is opposite to that in **b**.

Figure 2. Parabolic trajectories given by $dq/dm = \beta m$, a simulation of a one-synapse neuron receiving constant input $d_0 = 1$. Stable equilibrium states are indicated by ●. Note that states with $q(t=0) < q_a$ are driven to nontrivial ($m \neq 0$) final states. Functions σ_i of the form (6) were used for the two cases: **a** $\eta_2 > \eta_1$ and **b** $\eta_2 < \eta_1$.

Figure 3. This response curve illustrates the definition of selectivity given by (10) for a one-parameter (ω) stimulus environment. The domain of ω together with the response range (zero to the maximum M) determine a rectangle. The fraction of this rectangle which does not lie below the response curve is the selectivity of the response. (From Bienenstock et al., 1982, with permission)

Figure 4. Lines of constant selectivity for two 2-pattern environments, which have a maximum selectivity of 0.5 ($1-1/K$ for K patterns). Note that there is a line of maximum selectivity orthogonal to each pattern and that the line of zero selectivity is orthogonal to the *difference* between the patterns. **a** if the two patterns have a common norm, the locus of zero-selectivity lies midway between the patterns. **b** if they have different norms, the isoselectivity contours are skewed toward the weaker stimulus.

Figure 5. Curved surfaces give loci of nontrivial equilibria with respect to each of the stimuli in the 2-pattern environment $\mathbf{d}^1=(1,0)$, $\mathbf{d}^2=(0,1)$. Each surface is defined by translating the curved lines in Figure 2, in the direction orthogonal to the planes in which they lie. Assuming $q(t=0)$ is sufficiently small, the neuronal state converges to one of the following loci, each defined as the intersection of a $\phi(\mathbf{m}\cdot\mathbf{d}^1=0)$ surface and a $\phi(\mathbf{m}\cdot\mathbf{d}^2=0)$ surface. **a** S-cell: c_1 or c_2, contours defined by maximally selective states satisfying $\mathbf{m}\cdot\mathbf{d}=0$ for one pattern and $q=\theta^{-1}(\mathbf{m}\cdot\mathbf{d})$ for the other. **b** G-cell: c_{12} $(\mathbf{m}\cdot\mathbf{d}^1=\mathbf{m}\cdot\mathbf{d}^2=\theta(q))$, a contour consisting of minimally selective states.

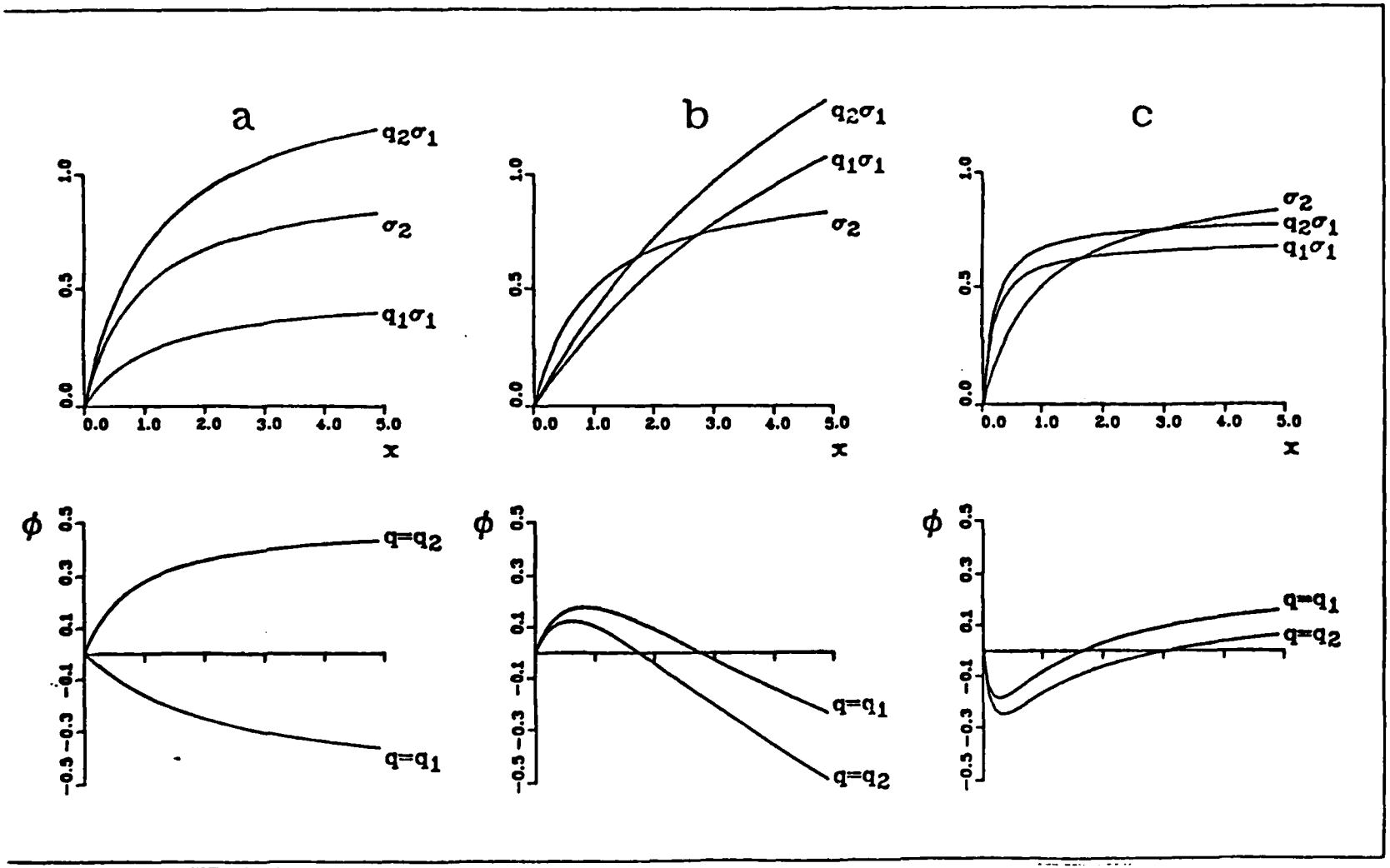
Figure 6. m-plane projections of trajectories are shown for the two-pattern environments of Figure 4: common norm – **a** S-cell: $W>0$, **b** G-cell: $W<0$; different norms – **c** S-cell, **d** G-cell.

Figure 7. Behavior of the model is shown in an environment that is periodic in one parameter. If the response generated by a particular stimulus gives a positive value for ϕ, then the resulting synaptic potentiation increases the response function over *all* patterns. The increase is a maximum for patterns in the same direction as the stimulus. This illustrates the notion of parallel modification (section 2.2.1). With sufficient exposure to the environment, the response curve thus becomes maximally selective for $W>0$ (upper figure) or minimally selective for $W<0$ (lower figure).

Figure 8. An environment that varies periodically over two independent parameters drives a initial random state having the response surface shown in **a** to the final state **b** for $W>0$, and to **c** for $W<0$. The stimulus set consisted of 400 patterns in a 20-dimensional space.

Figure 9. Contrast enhancement may be a primary task of generalization neurons. Here, several neurons share a set of afferents and can evolve such that the S-cells prefer various patterns while the G-cells provide inhibition uniformly across the environment, thus suppressing partially excited S-cells.

This circuit permits S-cells to attain much higher selectivities even with positive semidefinite input weights. ● : excitatory synapses ; —| : inhibitory synapses.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b
c
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σ_2
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x
ϕ
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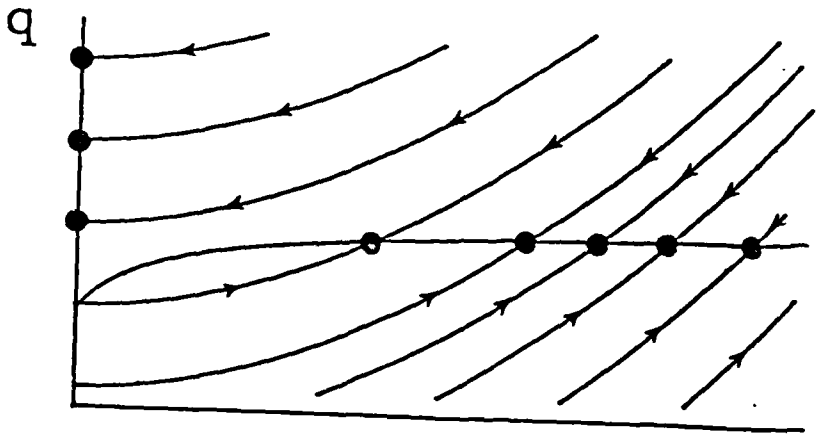
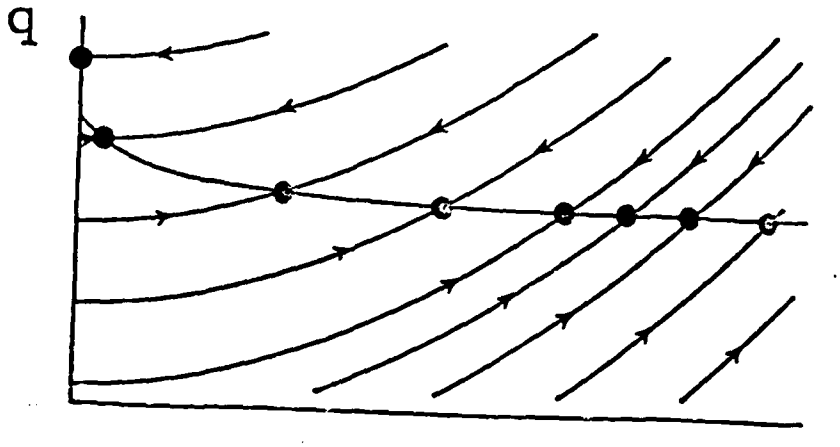
FIGURE 1

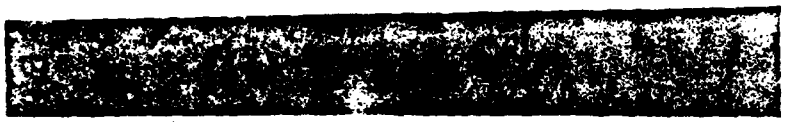


(a) $\eta_2 > \eta_1$



(b) $\eta_2 < \eta_1$

FIGURE 2



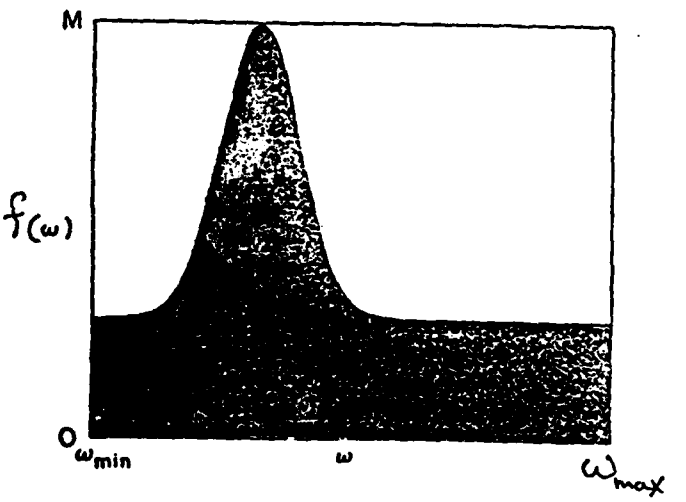


FIGURE 3

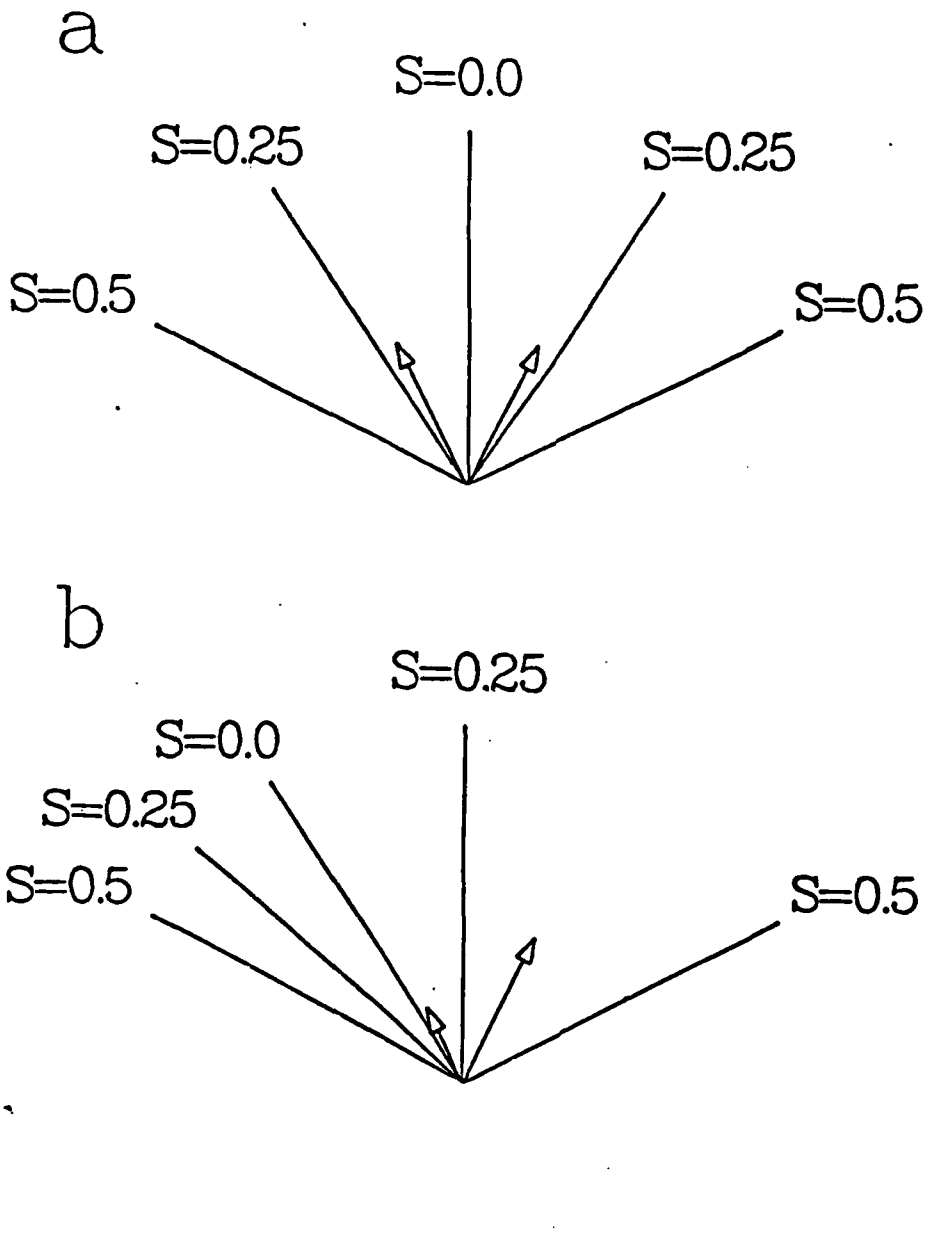
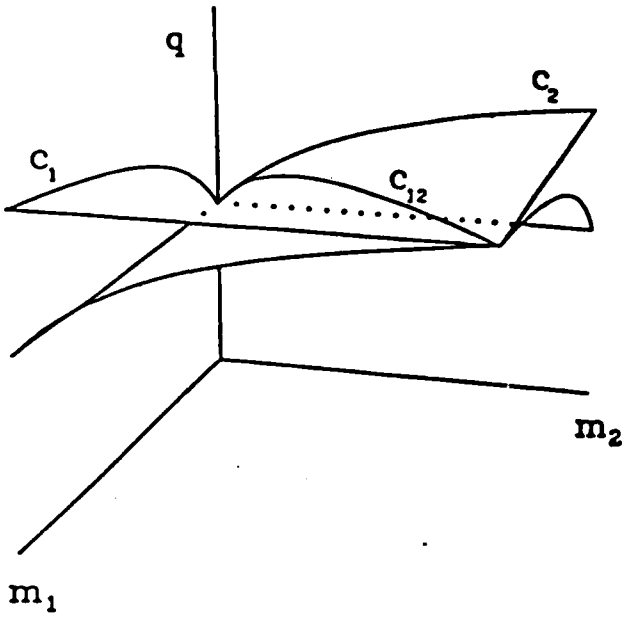
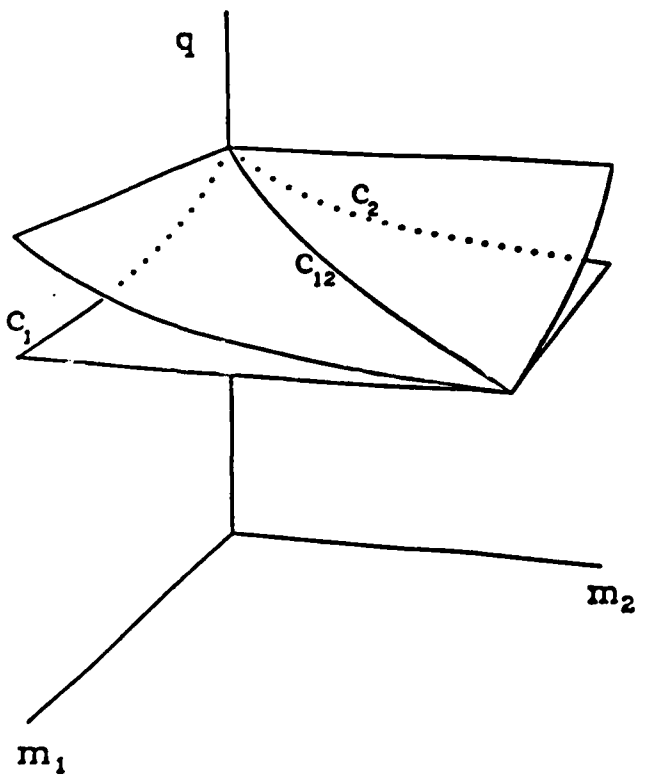


FIGURE 4

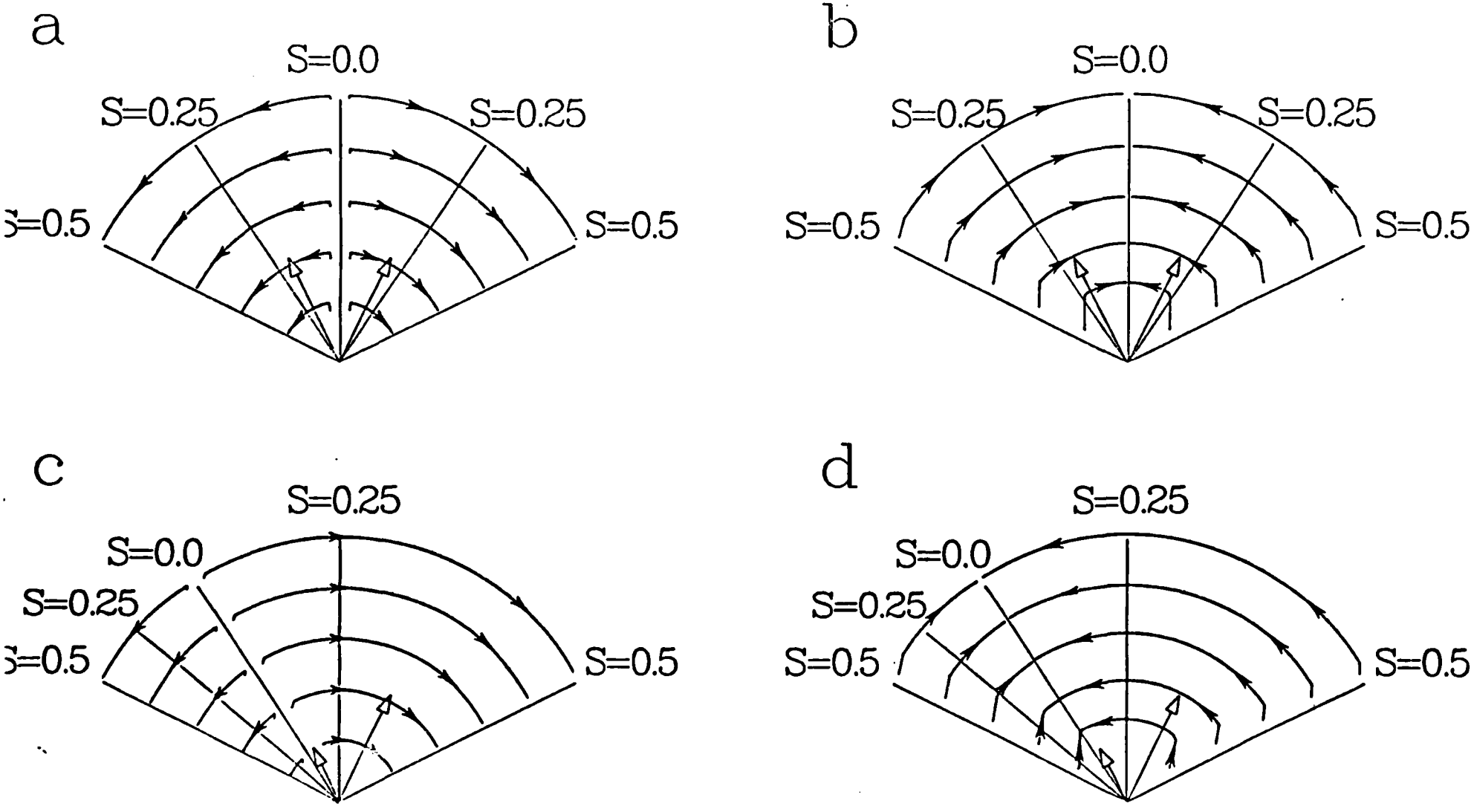


(a) $\eta_2 > \eta_1$



(b) $\eta_2 < \eta_1$

FIGURE 5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c
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S=0.25
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d
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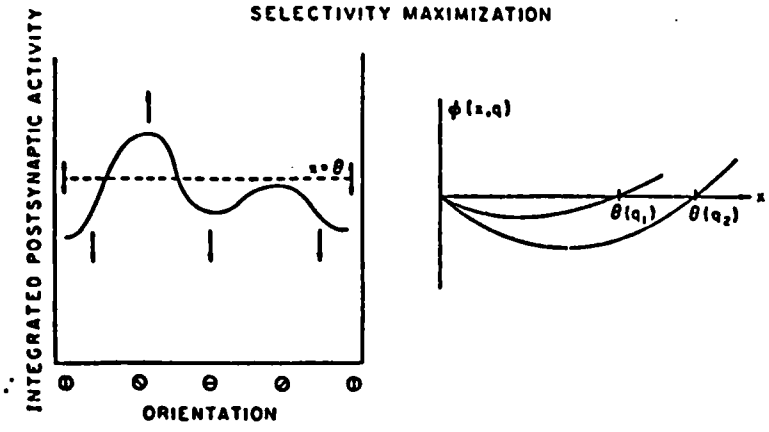
FIGURE 6


SELECTIVITY MAXIMIZATION
INTEGRATED POSTSYNAPTIC ACTIVITY
x=θ
ORIENTATION
φ(x,q)
θ(q1)
θ(q2)
x

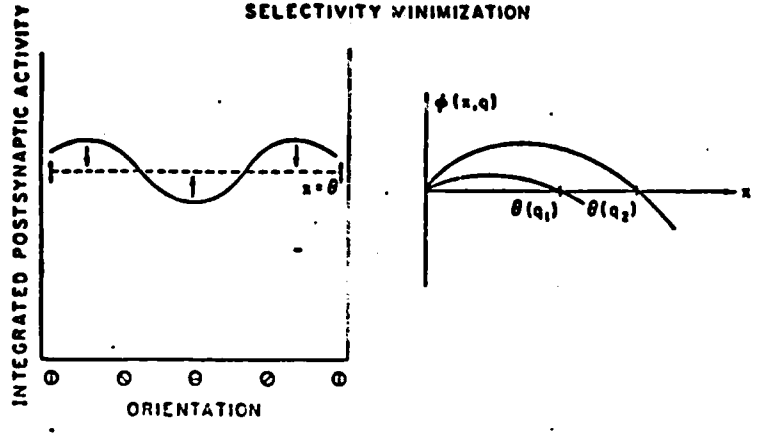
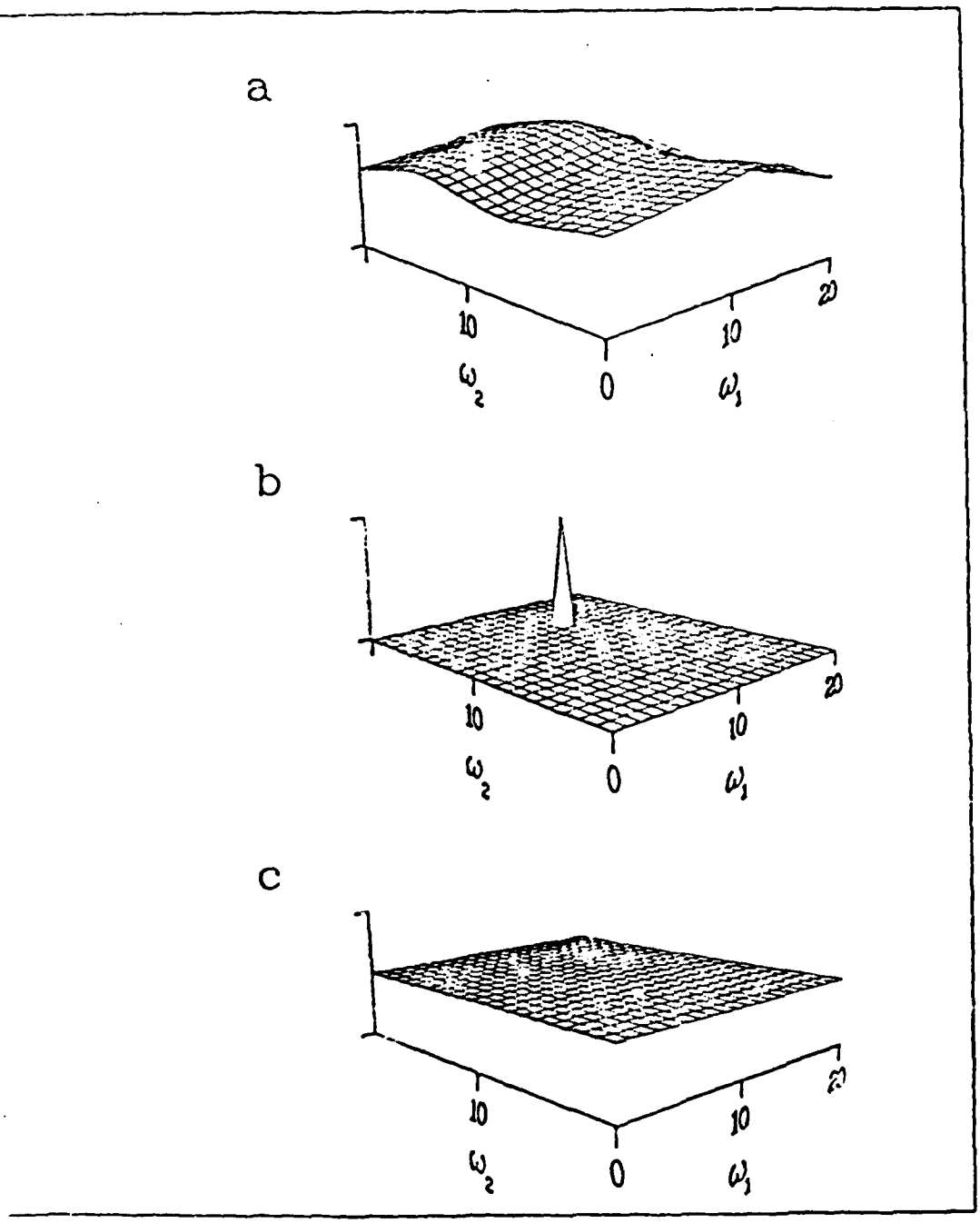

SELECTIVITY MINIMIZATION
INTEGRATED POSTSYNAPTIC ACTIVITY
x=θ
ORIENTATION
φ(x,q)
θ(q1)
θ(q2)
x

FIGURE 7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10
ω_2
0
10
ω_1
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b
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ω_2
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c
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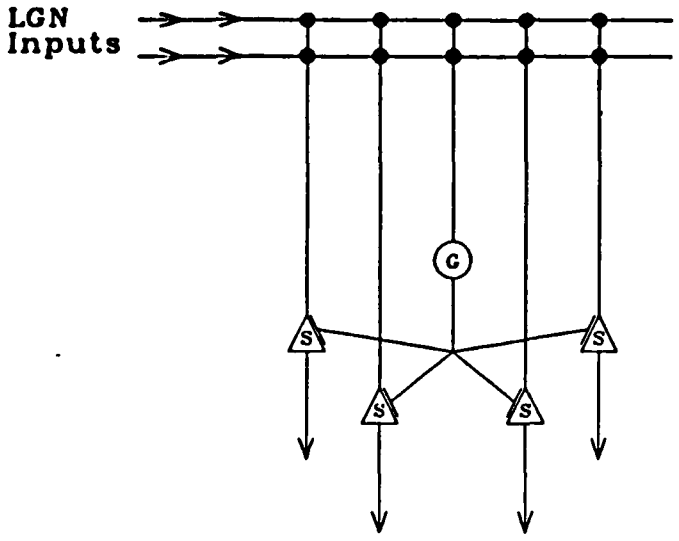
ω_2
0
10
ω_1
20

FIGURE 8

FIGURE 9



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